Environmental Controls on Soil and Whole-ecosystem Respiration from a Tallgrass Prairie

K. Franzluebbers, A. J. Franzluebbers,* and M. D. Jawson

ABSTRACT

Environmental controls on C cycling in terrestrial ecosystems are difficult to define, because (i) C fluxes from plant vs. microbial activity are difficult to separate, and (ii) controlling variables are often intercorrelated. We investigated temporal and spatial determinants of soil respiration and whole-ecosystem respiration using nighttime exposure of static chambers to alkali absorption during 2 yr on a tallgrass prairie in northeastern Kansas. Soil respiration (mg CO_2-C m^{-2} h^{-1}) was positively related to soil organic C (SOC, kg m^{-2} 0.1 m^{-1}) through linear regression [CO_2-C = −44 + (40 SOC), r^2 = 0.71]. Temporal variations in respiration were related to soil temperature, water-filled pore space (WFPS), and a plant growth rate function, with a combined R^2 of 0.76 for soil respiration and of 0.84 for whole-ecosystem respiration. Temporal variograms suggested that both soil and whole-ecosystem respiration became increasingly dissimilar the longer the time between measurements up to 30 d, while dissimilarity in soil temperature and WFPS leveled between 10 and 20 d of separation. A plant growth rate function was an important variable that controlled whole-ecosystem respiration, as well as soil respiration. The ratio of soil respiration to whole-ecosystem respiration was ≈0.4 during maximum plant growth (July) and approached a value of 1 during minimal plant growth (November to March). We conclude that whole-ecosystem respiration is under similar environmental controls as soil respiration, the main variables being soil organic C, soil temperature, WFPS, and plant growth rate, which all control the supply of readily mineralizable substrates.

Grasslands cover 24% of the terrestrial surface (Sims and Risser, 2000) and vary with respect to species composition, net primary productivity, abiotic environment, and management, all of which affect decomposition and sequestration of organic matter. Region-specific information is needed to characterize C fluxes in these vast land areas in order to better quantify the role of grasslands in greenhouse gas emissions and potential C sequestration (Scurlock and Hall, 1998). Information exists on net ecosystem exchange of CO_2 in tallgrass prairies (Verma et al., 1989; Kim and Verma, 1990; Kim et al., 1992; Polley et al., 1992), as well as some information on soil respiration in this ecosystem (Kucera and Kirkham, 1971; Ham et al., 1995; Bremer et al., 1998; Knapp et al., 1998b; Mielnick and Dugas, 2000), but relatively little information is available on soil respiration measured in concert with whole-ecosystem respiration.

Carbon fluxes in terrestrial ecosystems are dominated by (i) biochemical fixation of CO_2 via photosynthesis and (ii) biochemical release of CO_2 via autotrophic plant respiration and heterotrophic microbial respiration. Net ecosystem exchange of CO_2 as an integration of photosynthesis, plant dark respiration, and soil respiration in grasslands can be obtained with various micrometeorological techniques, which integrate across large land areas (Verma, 1990; Norman et al., 1992). Knowing the contribution of soil respiration to these fluxes would improve our understanding of the C cycle and help determine rates of ecosystem C sequestration. Separation of soil respiration from whole-ecosystem respiration is best suited during the nighttime, when photosynthetic fixation of CO_2 is not a factor. There is also a need to better understand whole-ecosystem respiration during the nighttime, since micrometeorological techniques for net ecosystem exchange of CO_2 are generally less suited during the nighttime than during the daytime, because of less reliable energy balance, concentration gradients, and wind speeds needed for calculations (Harper, 1989).

Previous studies have indicated a high degree of spatial and temporal variability in soil respiration that makes extrapolations of findings to different ecosystems difficult (Buyanovsky et al., 1986; Kiefer, 1990; Rochette et al., 1991). Even when attempting to extrapolate results within an ecosystem, major errors may occur because of the limited frequency of observations collected mainly in the summer during active plant growth, at certain times of the day, or with measurement techniques that disturb the natural system by removal of vegetation. The frequency of observations needed to estimate soil and whole-ecosystem respiration for a specific period of interest will depend on the day-to-day variability in environmental conditions (i.e., temperature and moisture), which affect respiration. We hypothesized that variograms could be used as a means of describing the temporal variability of respiration in order to determine a reasonable sampling frequency.

Our primary objective was to elucidate whether environmental (i.e., soil organic C, soil temperature, and WFPS) and physiological (i.e., plant growth rate) factors controlled soil respiration and whole-ecosystem respiration to the same extent. Secondly, we wanted to determine an optimum sampling frequency for soil and whole-ecosystem respiration within a year.

MATERIALS AND METHODS

Site and Vegetation

This study was conducted in 1987 and 1988 at the Konza Prairie, a tallgrass prairie in northeastern Kansas, 14 km south of Manhattan (39°3′ N, 96°32′ W, 445 m above mean sea level). The site was grazed for several years prior to 1986, at which

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Abbreviations: DOY, day of year; SOC, soil organic carbon; WFPS, water-filled pore space.

Table 1. Soil characteristics (0–10 cm) of the five locations at the Konza Prairie site.

Location	Series	pH	CCE†	Total N	SOC‡	P	K	Sand	Clay	D_b
				g kg^{-1}		mg kg^{-1}		g kg^{-1}		Mg m^{-3}
A	Dwight	6.1	55	3.13	39.6	4.4	374	81	337	1.03
B	Dwight	6.2	65	3.32	42.8	3.3	342	84	369	0.98
C	Dwight	6.2	55	2.88	36.8	4.4	332	76	344	1.02
D	Irwin	5.9	49	2.25	28.5	3.2	165	103	286	1.12
E	Irwin	6.0	55	2.76	35.0	4.1	272	92	313	1.05

† CCE = calcium carbonate equivalent.
‡ SOC = soil organic carbon.

time a 6.3-ha area was fenced to exclude cattle. The area was burned annually, and latest events prior to our observations were 16 April 1987 and 15 April 1988. Additional information on the Konza Prairie can be found in Knapp et al. (1998a).

Five locations, separated by 130 ± 65 m, within the fenced area were randomly chosen for sampling. Three of the locations were on Dwight silty clay loam (fine, smectitic, mesic Typic Natrustolls) and two were on Irwin silty clay loam (fine, mixed, mesic Pachic Argiustolls). Soil characteristics of the five locations were determined by the Soil Testing Service of the University of Nebraska [soil pH (1:1 soil:water), Ca carbonate equivalent (manometric method), total N (Kjeldahl analysis), soil organic C (acid dichromate titration), P (Bray-1), K (neutral NH_4OAc extraction), and sand and clay (hydrometer method)] (Table 1).

Plant species composition was estimated during the dominant flowering stage of 1987 with the modified step point method (Owensby, 1973). Vegetation was dominated by warm-season perennial grasses, including 27% big bluestem (*Andropogon gerardii* Vitman), 22% indiangrass [*Sorghastrum nutans* (L.) Nash], and 17% switchgrass (*Panicum virgatum* L.). The remainder of the community was composed of numerous other grasses, sedges, forbs, and woody plants.

Measurement of Soil and Whole-Ecosystem Respiration

Soil respiration and whole-ecosystem respiration were determined during nocturnal exposure using a static chamber method with alkali absorption (Zibilske, 1994). Measurements were made during the nighttime to avoid shading of the soil and heating of the chamber atmosphere during the day. Nocturnal measurements also avoided complications in interpretation of whole-ecosystem respiration if the canopy were shaded by the chamber during daytime photosynthetic activity. The static chamber method with alkali absorption allowed an integrated estimate of respiration during 8- to 12-h exposure periods, which was converted to an hourly rate (i.e., mg CO_2-C m^{-2} h^{-1}) for comparison among sampling times.

Soil respiration was determined using metal cylinders (6.7 cm diam., 13 cm height) inserted 0.5 to 1.0 cm into soil in small bare spots immediately adjacent to clumps of grass. A glass sample vial containing 10 mL of 1 *M* KOH was hung in the chamber by a wire held in place by a rubber stopper. Surface area of the alkali was 12 cm^2. Within each of the five locations, three to four chambers in 1987 and five chambers in 1988 were set out randomly within an area of ≈4 m^2. Chambers were placed 10 to 90 min prior to sunset and removed 20 min before to 40 min after sunrise.

Whole-ecosystem respiration was determined using aluminum sheet-metal chambers (30 cm × 30 cm surface area, 40 cm height). The bottom edge of the chamber had a lip of 2.5 cm in width covered with a rubber gasket that was sealed with clamps to a permanently installed frame, which was inserted in soil to a depth of 2 to 3 cm. Two plastic containers with 100 mL of 1 *M* KOH each were supported by two 23-cm high tripods within the chamber. Total surface area of the alkali was 183 cm^2. A 10-cm long copper tube (0.4-cm inside diam.) supported by a rubber septum on top of the chamber allowed for equal air pressure inside and outside the chamber. At each of the five locations, one chamber was placed in 1987 and three chambers were placed in 1988.

Blanks from each of the two chamber types were sealed at the bottom and not exposed to soil at each of the measurement periods. Blanks, which were determined identically to exposed samples, accounted for residual CO_2 absorbed from the atmosphere during the measurement period and during sample handling and titration. Alkali was titrated with 0.25 and 2 *M* HCl for the 10-mL and 200-mL samples, respectively. The quantity of absorbed CO_2 was determined by titration to a phenolphthalein endpoint following precipitation of the absorbed CO_2 to $BaCO_3$ with addition of excess $BaCl_2$ (Zibilske, 1994). Soil and whole-ecosystem respiration were calculated based on exposure time and soil surface area.

Soil respiration and whole-ecosystem respiration were determined simultaneously four to five times per week from 2 June to 22 August 1987 (n = 51) and less frequently (i.e., ≈10-d intervals) from 6 March to 15 November 1988 (n = 29). Samples were not collected in winter due to snow cover and inability to insert chambers in frozen soil.

Methodological approaches for assessing soil respiration are diverse, with variations in analytical technique (i.e., static vs. dynamic chamber techniques, alkali absorption vs. infrared gas analysis, and undisturbed vegetation vs. various vegetation avoidance techniques). Some methodological comparison studies have found the static chamber method with alkali absorption to give lower values compared with dynamic chamber methods under conditions of high soil respiration (Freijer and Bouten, 1991; Nay et al., 1994). However, quantitative field measurements with the dynamic chamber method can sometimes yield unrealistically high daily flux estimates. For example, soil respiration using a dynamic chamber method (<2 min measurements made in the daytime) suggested 100% decomposition of maize (*Zea mays* L.) residue in only 11 d, while soil respiration using a static chamber method (alkali absorption during 24-h exposures) suggested 30% decomposition of maize residue during 4 mo, the latter being more realistic (Jensen et al., 1996). Ham et al. (1995) found that the rate of soil respiration estimated with a small dynamic chamber method was nearly equivalent to that of whole-ecosystem respiration under a large dynamic chamber, suggesting that aboveground plant dark respiration of live biomass would have been negligible, which is certainly not reasonable. No difference in respiration rate was observed between two static chamber methods with 24-h exposure to alkali or with 30-min exposure and measuring the increase in headspace CO_2 concentration (Raich et al., 1990). This lack of difference indicated quantitative absorption of CO_2 by alkali without creating an increase in CO_2 flux by increasing the concentration gradient between chamber atmosphere and soil. An advantage of the static chamber method with alkali absorption is that an esti-

mate integrated from several hours to a day can be obtained, which would be achievable with the dynamic chamber method only if an expensive automated system were available that might preclude sufficient replication.

Soil Physical Conditions

Gravimetric soil water content at 0- to 5- and 5- to 10-cm depths was determined in the morning after each exposure during 1987 and in the evening before each exposure during 1988. Three soil cores were collected at each location at a maximum distance of 1.5 m from chambers, composited, and oven-dried (105°C, 48 h). Soil temperature at a 7-cm depth was determined with a thermocouple at two spots within each of the five locations in the evening and in the morning, which were then averaged. These two time periods approximated daily minimum and maximum temperature at 7 cm. Soil bulk density was determined at each of the five locations from duplicate cores (5.4-cm diam.) at depths of 0 to 3 and 5 to 8 cm on 13 October 1987. Water-filled pore space was calculated as:

$$\text{WFPS} = \text{SWC} \times D_b/(1 - D_b/\text{PD})$$

where, SWC is soil water content (kg kg^{-1}), D_b is bulk density (Mg m^{-3}), and PD is particle density (assumed to be 2.65 Mg m^{-3}) (Doran et al., 1988).

Statistical Analyses

The relationship of soil and whole-ecosystem respiration with soil organic C was evaluated with simple linear regression. For multiple regression analysis, data from soil respiration, whole-ecosystem respiration, soil temperature, and WFPS were averaged across the five locations for each day of measurement prior to regression analyses within each year. Water-filled pore space of the 0- to 10-cm depth was used as the moisture variable in all analyses, as this property integrates porosity and moisture variables (Doran et al., 1988; Franzluebbers, 1999). The effect of soil temperature on respiration was linearized with a Q_{10} function, assuming an optimum at 30°C and doubling with every 10°C change in temperature (Kucera and Kirkham, 1971):

$$\text{temperature function} = 2^{[(°\text{C} - 30)/10]}$$

A plant growth rate function was included in the multiple regression analysis to express the temporal course of plant-derived respiration (i.e., autotrophic root respiration and heterotrophic rhizosphere respiration) from soil and additionally, aboveground plant dark respiration from vegetation using a Gaussian equation of the form (Superior Performing Software Systems, 1998):

$$\text{plant growth rate function} = \text{A} \times e^{[-0.5[(\text{DOY} - \text{X})/\text{B}][(\text{DOY} - \text{X})/\text{B}]]}$$

where, A is the magnitude of the peak (derived from multiple regression), DOY is the independent variable for day of year, X is the DOY at the apex [determined from several iterations and set as 1 July (DOY 183) for all equations], and B is a constant (determined from several iterations and set as 33 for all equations). Soil respiration and whole-ecosystem respiration were regressed upon independent variables of temperature, WFPS, temperature × WFPS interaction, and plant growth rate for each year separately and for combined years using SAS (SAS Institute, 1985). Aboveground plant dark respiration was calculated as the difference between whole-ecosystem respiration and soil respiration. This calculated value was subjected to a separate regression analysis to identify the importance of physiological vs. environmental variables on soil and whole-ecosystem respiration. Goodness of fit from predictions with each of these regression equations against actual values was evaluated by coefficients of determination, paired t-tests of multiple observations within a year, and comparison of means. Effects at $P \leq 0.1$ were considered significant.

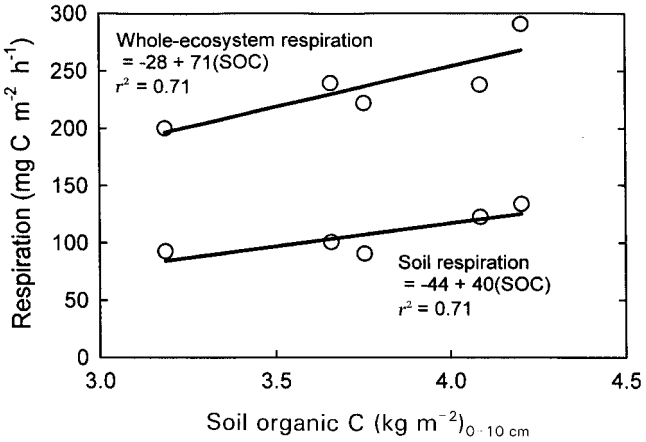

Fig. 1. Mean soil respiration and whole-ecosystem respiration in relationship with soil organic C content. Each point represents the mean of 79 observations during 2 yr.

Temporal variograms were constructed for soil respiration, whole-ecosystem respiration, soil temperature, and WFPS us-

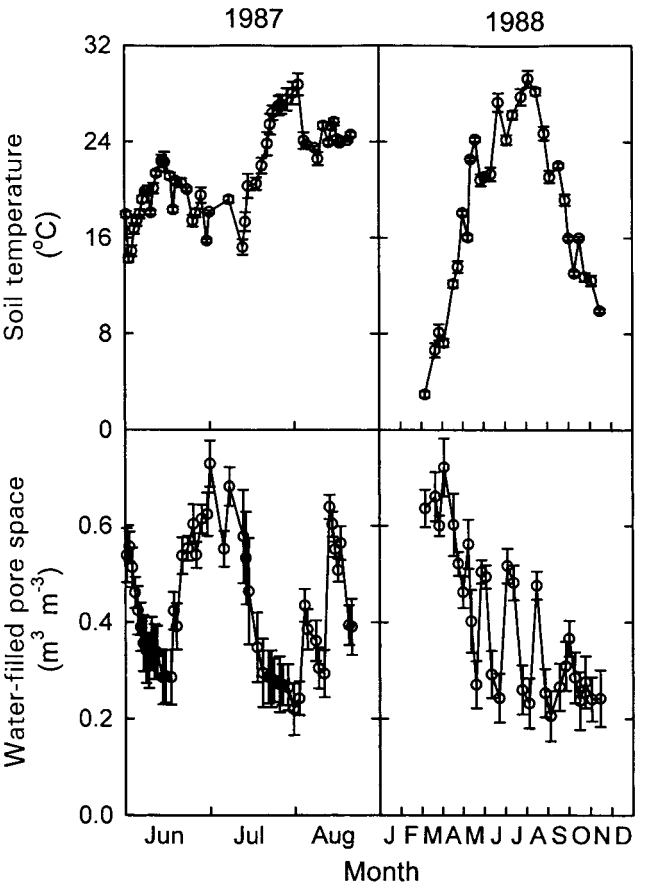

Fig. 2. Soil temperature and water-filled pore space measured during 1987 and 1988. Error bars represent standard deviation among five replicates for each sampling point.

Table 2. Soil respiration (mg CO_2-C m^{-2} h^{-1}) as predicted by soil temperature (T) {i.e., linearized transformation from $2^{[(°C - 30)/10]}$} water-filled pore space (WFPS), and plant growth rate in 1987 (1 June to 21 August, $n = 50$), in 1988 (6 March to 14 November, $n = 29$), and in both years combined ($n = 79$).

	1987		1988		Combined years	
Property	**Coefficient**	**$P > \|t\|$**	**Coefficient**	**$P > \|t\|$**	**Coefficient**	**$P > \|t\|$**
			Source of variation in soil respiration			
Intercept	**69.7**	**0.224**	**96.3**	**0.001**	**91.6**	**0.005**
T	**−82.7**	**0.351**	**−211**	**<0.001**	**−242**	**<0.001**
WFPS	**236**	**0.079**	**−179**	**0.002**	**−150**	**0.004**
T × WFPS	**54.1**	**0.815**	**675**	**<0.001**	**741**	**<0.001**
Plant growth, 1987	**−5.16**	**0.846**	**NA**	**NA**	**92.1**	**<0.001**
Plant growth, 1988	**NA**	**NA**	**80.0**	**<0.001**	**77.2**	**<0.001**
			Summary statistics			
R^2	**0.707**		**0.844**		**0.760**	
Root mean square error	**28**		**20**		**29**	
Mean soil respiration	**132**		**68**		**108**	

NA = not applicable.

ing data from 1987 to evaluate the daily self-dependence of these properties (Warrick et al., 1986). The number of paired comparisons was 23 ± 5 for each of the days of separation up to 30 d.

RESULTS AND DISCUSSION

Effect of Soil Organic C on Respiration

Mean soil respiration and whole-ecosystem respiration were linearly related to soil organic C (Fig. 1). Both types of respiration were also positively related to total N, Ca carbonate equivalent, and clay content, and negatively related to soil bulk density. These abiotic variables were highly correlated to soil organic C concentration (e.g., $r = 0.99$ with total N, $r = 0.89$ with calcium carbonate equivalent, $r = 0.96$ with clay content, and $r = -0.97$ with soil bulk density). Soil organic C was thought to be the dominant factor controlling in situ respiration, since it is a substrate for heterotrophic activity. Additional plant residue C produced under more fertile soils would be partitioned into labile (i.e., microbially accessible and transformed into CO_2) and stable (i.e., microbially resistant and transformed into soil organic C) fractions (Parton et al., 1988). Therefore, more fertile soils would be able to store more soil organic C and release more CO_2 to the atmosphere compared with less fertile soils, on an equivalent area basis.

Influence of Environmental Conditions on Respiration in 1987

Soil underwent three major drying periods following peak moisture contents in early June, early July, and mid-August in 1987 (Fig. 2). Soil respiration responded to changes in WFPS, but not significantly to changes in temperature or plant growth rate (Table 2). Because of the limited range in soil temperature during measurement periods in 1987 (i.e., from 14 to 29°C), temperature had relatively little impact on soil respiration. Whole-ecosystem respiraton, however, responded significantly to changes in all three environmental variables investigated (Table 3).

Temporal variance in soil respiration in 1987 increased rapidly up to 10 d of separation and less rapidly thereafter (Fig. 3). A similar increase in temporal variance of soil temperature up to 10 d of separation, with some stabilization from 10 to 20 d of separation, was observed. Temporal variance in WFPS increased up to 20 d of separation, while temporal variance in whole-ecosystem respiration increased linearly up to 30 d of separation. These temporal variograms indicate strong autocorrelation of soil properties during time separations of at least 10 d. These relationships also indicate that assessments of environmental controls on respiration throughout the year might be best obtained with sampling intervals of

Table 3. Whole-ecosystem respiration (mg CO_2-C m^{-2} h^{-1}) as predicted by soil temperature (T) {i.e., linearized transformation from $2^{[(°C - 30)/10]}$} water-filled pore space (WFPS), and plant growth rate in 1987 (1 June to 21 August, $n = 46$), in 1988 (6 March to 14 November, $n = 29$), and in both years combined ($n = 75$).

	1987		1988		Combined years	
Property	**Coefficient**	**$P > \|t\|$**	**Coefficient**	**$P > \|t\|$**	**Coefficient**	**$P > \|t\|$**
			Source of variation in whole-ecosystem respiration			
Intercept	**203**	**0.059**	**106**	**0.060**	**200**	**<0.001**
T	**−509**	**0.003**	**−228**	**0.037**	**−473**	**<0.001**
WFPS	**−255**	**0.310**	**−278**	**0.015**	**−339**	**0.003**
T × WFPS	**1156**	**0.012**	**1225**	**<0.001**	**1286**	**<0.001**
Plant growth, 1987	**301**	**<0.001**	**NA**	**NA**	**288**	**<0.001**
Plant growth, 1988	**NA**	**NA**	**125**	**0.004**	**245**	**<0.001**
			Summary statistics			
R^2	**0.778**		**0.866**		**0.844**	
Root mean square error	**50**		**42**		**52**	
Mean respiration	**293**		**144**		**235**	

NA = not applicable.

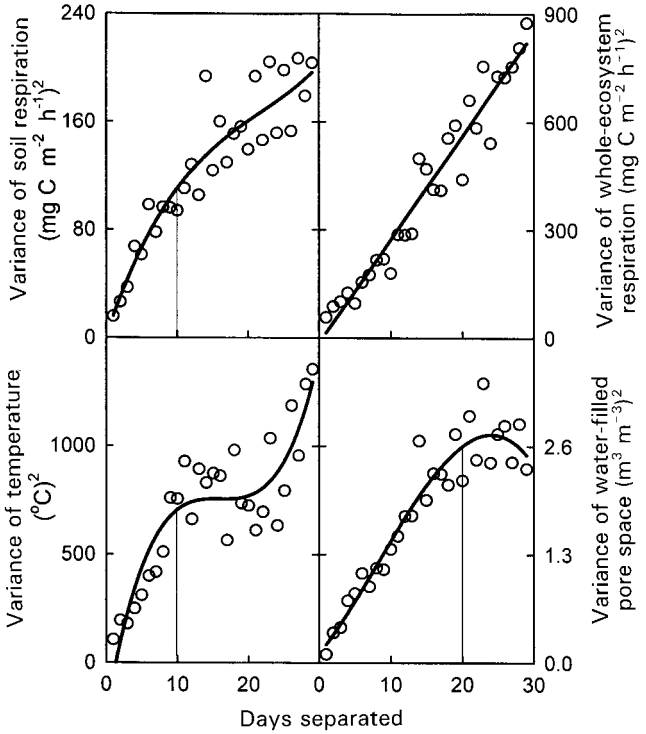

Fig. 3. Variances of soil respiration, whole-ecosystem respiration, soil temperature, and water-filled pore space when observations were separated from 1 to 29 d apart from each other in 1987. Vertical lines mark the points of inflection that occurred at 10 and 20 d of separation. Regression lines are polynomial expressions.

≈10 d, rather than more frequently if total sample number were limited. In 1988 therefore, we sampled every 9 ± 3 d during a 254-d period, compared with every 2 ± 1 d during an 82-d period in 1987.

Influence of Environmental Conditions on Respiration in 1988

The range in WFPS during sampling events in 1988 was similar to that in 1987, but the range in soil temperature in 1988 was much greater than in 1987 because of the expanded sampling period (Fig. 2). Water-filled pore space was high in early spring of 1988 due to overwinter soil moisture recharge. Variation in WFPS was large throughout the summer, capturing alternately dry and wet periods, although WFPS never exceeded 0.6 m^3 m^{-3} as it did during two phases in 1987 (Fig. 2 and 4). Observed soil respiration and whole-ecosystem respiration were generally lower during the summer of 1988 than in 1987, because of the generally drier conditions during the summer of 1988.

Soil respiration and whole-ecosystem respiration in 1988 responded significantly to soil temperature, WFPS, and plant growth rate (Table 2 and 3). Root mean square errors of regressions were relatively similar in both years, despite ≈50% lower soil respiration (Table 2) and whole-ecosystem respiration (Table 3) in 1988. The coefficient of variation from our regression equations was 21% in 1987 and 29% in 1988, which was considerably less than the coefficient of variation of 39% reported for soil respiration from a tallgrass prairie in

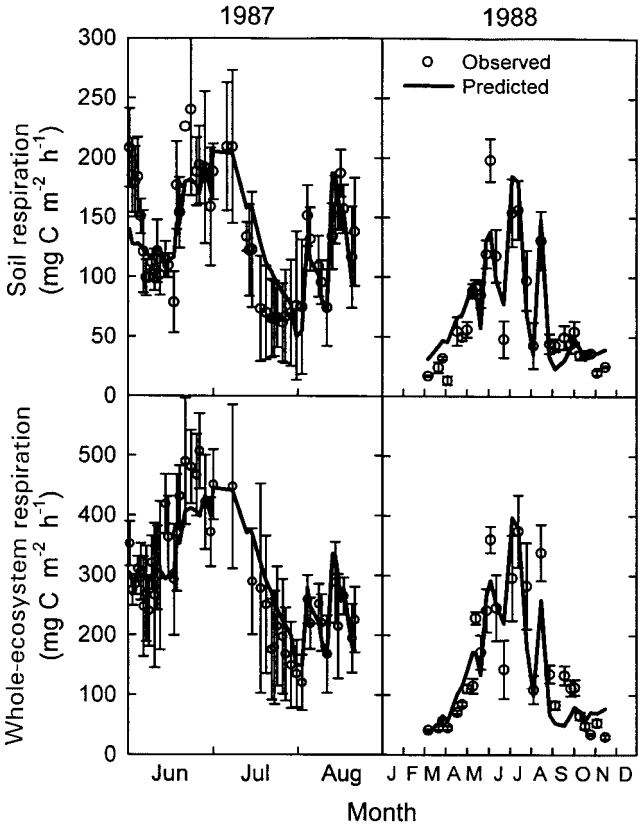

Fig. 4. Soil respiration and whole-ecosystem respiration measured during 1987 and 1988. Predicted respiration was from the combined years multiple regression in Table 2 for soil respiration and in Table 3 for whole-ecosystem respiration. Error bars represent standard deviation among 5 replicates for each sampling point.

Texas (Mielnick and Dugas, 2000). The study in Texas included moisture and temperature variables, but no plant growth variable, which appears to be an important variable describing seasonal C input.

Yearly Variations in Soil and Whole-Ecosystem Respiration

During the summer months of June through August, soil respiration was 133 ± 50 mg CO_2-C m^{-2} h^{-1} in 1987 and 110 ± 56 mg CO_2-C m^{-2} h^{-1} in 1988 (mean ± standard deviation among observations within a year). Soil respiration during the summer months in a tallgrass prairie in Missouri was 104 ± 15 mg CO_2-C m^{-2} h^{-1} (Kucera and Kirkham, 1971). The temporal variation in soil respiration implies strong environmental controls from temperature and soil water on autotrophic and heterotrophic respiration, as well as from physiological controls (i.e., C fixation and allocation) on plant growth rate.

We attempted to validate regression equations developed from individual years with actual data collected in the other year and found (i) predictions of respiration in 1987 with the equation developed in 1988 were poor for both soil respiration ($r^2 = 0.54$, $n = 49$) and whole-ecosystem respiration ($r^2 = 0.33$, $n = 45$) and (ii) predictions of respiration in 1988 with the equation developed in 1987 were even poorer (data not shown). Measurements made during a limited time of the year (e.g.,

summer sampling as in 1987) did not appear to yield a true reflection of the importance of independent variables that controlled respiration throughout the year. If 1987 were the only data set available, the negative coefficient describing the effect of plant growth rate on soil respiration (Table 2) suggested that soil respiration would be higher in spring and fall than in summer. This effect could have been misinterpreted had we not measured during a greater portion of the year in 1988.

Combined Years Regression of Soil and Whole-Ecosystem Respiration

The combined years regression equations tended to underpredict the high observations of soil respiration and whole-ecosystem respiration during June of 1987 (Fig. 4). Otherwise, the extreme fluctuations in soil respiration and whole-ecosystem respiration observed in August of 1987 and in May through August of 1988 were closely matched with predictions from the combined years regression equations. These fluctuations were effectively explained with variations in temperature, WFPS, and plant growth rate.

Soil temperature × WFPS interactions were highly significant for both soil respiration (Table 2) and whole-ecosystem respiration (Table 3). Increasing soil temperature had little effect on soil respiration and whole-ecosystem respiration at low and medium levels of WFPS, but positively influenced soil respiration and whole-ecosystem respiration at high WFPS (Fig. 5a,d). Conversely, WFPS had little effect on soil respiration and whole-ecosystem respiration at low and medium levels of soil temperature, but increasing WFPS had positive influences on soil respiration and whole-ecosystem respiration at high soil temperatures. These interactions indicate that falling below base levels of either temperature (≈10°C) or WFPS (≈0.4 $m^3\ m^{-3}$) would subdue or negate the expected positive response in respiration if improvements in the other controlling variable were to occur.

Including plant growth rate in the regression equation displaced part of the temperature effect that is intimately linked with plant growth, since the general temperature trend is similar to that of the plant growth rate function. Therefore, only the residual variation in temperature not associated with the seasonal plant growth function was included in the soil temperature variable. This residual variation in soil temperature had a relatively minor effect on soil respiration and whole-ecosystem respiration (Fig. 5), although it was still significant (Tables 2 and 3). The combined years regression equation could be a useful tool to predict soil respiration or whole-ecosystem respiration in other years or in the same year on unsampled days if environmental conditions were known.

Soil respiration in our study was higher than the 4 to 42 mg CO_2-C $m^{-2}\ h^{-1}$ observed from June to October in a mixed grassland (Redmann, 1978b). This would be expected based on the overall lower soil temperature and moisture conditions in Saskatchewan than in Kansas. Multiple regression equations including soil temperature, soil moisture, and precipitation accounted for 66 to 74% of variation (Redmann, 1978b), which was roughly

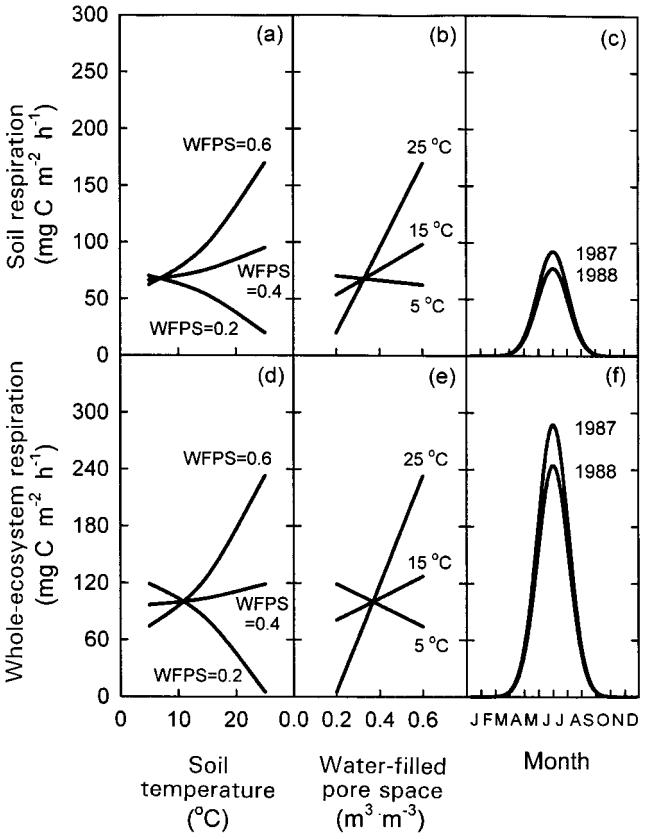

Fig. 5. Effect of changes in soil temperature at three levels of water-filled pore space ($m^3\ m^{-3}$) on soil respiration (a) and whole-ecosystem respiration (d). Effect of changes in water-filled pore space at three levels of soil temperature on soil respiration (b) and whole-ecosystem respiration (e). Effect of plant growth rate as a function of day of year on soil respiration (c) and whole-ecosystem respiration (f) in 1987 and 1988. Regression coefficients for parameters are in Table 2 for soil respiration and in Table 3 for whole-ecosystem respiration.

similiar to the explainable variation in our study. In contrast to our study, whole-ecosystem respiration at the Saskatchewan mixed grassland was poorly explained by temperature and moisture variables, that is, their multiple regression equation explained only 27% of total variation (Redmann, 1978a).

From a nearby location on the same tallgrass prairie in Kansas, Bremer et al. (1998) reported soil respiration of 230 ± 150 mg CO_2-C $m^{-2}\ h^{-1}$ from 31 measurements during a one-year period using a dynamic chamber technique with infrared gas analysis during 4-h exposures in the afternoon. From the soil temperature at 10 cm, WFPS at 0 to 10 cm, and DOY reported in Bremer et al. (1998), we predicted soil respiration using our combined years regression equation (Fig. 6). Predicted soil respiration was highly related to their observed values of soil respiration ($r^2 = 0.76$, $n = 31$), however these predictions were only 0.77 ± 0.24 of observed soil respiration reported in Bremer et al. (1998). The difference between predicted and observed values may have been due to depth of soil temperature measurement, time of day when measurements were taken, and measurement method. Soil temperature at 10 cm would likely have been lower than at 7 cm in the summer,

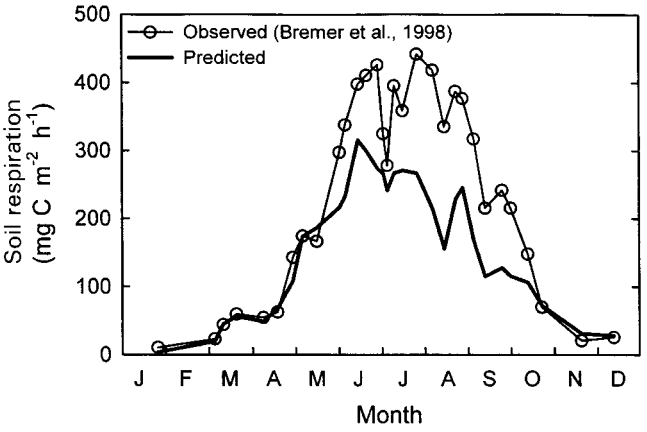

Fig. 6. Observed soil respiration at a nearby prairie location during 1996 to 1997 (Bremer et al., 1998) and predicted values from the combined years regression equation in Table 2.

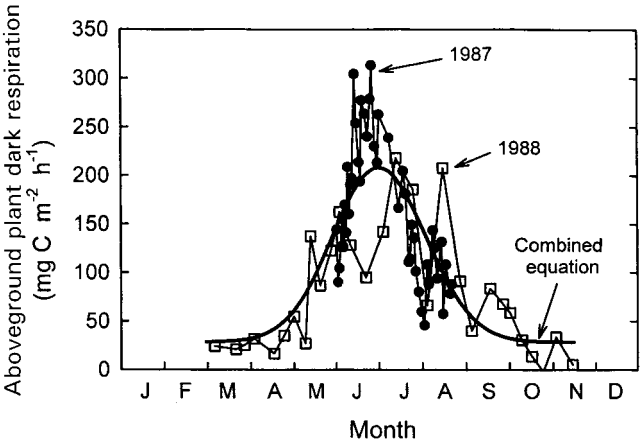

Fig. 7. Calculated aboveground plant dark respiration in 1987, 1988, and predicted from the difference in combined years regression equation between whole-ecosystem and soil respiration.

resulting in lower values of soil respiration using our equation. Soil temperature at 7 cm was 1 to 3°C higher during daytime exposures than during nighttime exposures, resulting in an average of 20% greater soil respiration during the day than during the night (Grahammer et al., 1991). It is also possible that the 60 ± 29% greater soil respiration reported by Bremer et al. (1998) during the June to September period, compared with predictions from our combined years regression equation, was due to (i) the use of a dynamic chamber technique or (ii) measurements made during midafternoon when a large quantity of photosynthates were being produced and translocated belowground. Root respiration can be up to 50% higher when exposed to photosynthetically active radiation than without (Osman, 1971). At high soil respiration rates, the dynamic chamber method has resulted in higher estimates than the static chamber method with alkali absorption (Rochette et al., 1992; Nay et al., 1994; Jensen et al., 1996). From November through May when plant growth was minimal, our predictions were 0.95 ± 0.27 of observed soil respiration in the study of Bremer et al. (1998). Despite the many differences in experimental conditions between our study and that of Bremer et al. (1998), our regression equation was able to closely mimic relative changes in soil respiration caused by changes in soil temperature, WFPS, and plant growth rate.

Plant Growth Rate

The combined years regression models attributed 33% of explained variation to the plant growth rate effect on soil respiration and 53% on whole-ecosystem respiration. The coefficient of variation in soil respiration was reduced from 38 to 27%, following the inclusion of the plant growth rate function (Table 2). Similarly, the coefficient of variation in whole-ecosystem respiration was reduced from 44 to 22% by including this function in the regression (Table 3). For soil respiration, the plant growth rate effect was likely due to responses in root respiration and microbially stimulated rhizosphere respiration. For whole-ecosystem respiration, an additional source included aboveground plant dark respiration.

The ratio of soil respiration to whole-ecosystem respiration was 0.45 ± 0.12 in 1987 and 0.51 ± 0.17 in 1988. These ratios compare favorably with observations of 0.54 to 0.64 in tundra soils from Alaska (Peterson and Billings, 1975), 0.40 in a mountain meadow in Austria (Cernusca et al., 1978), and 0.65 to 0.80 in a successional grassland in Germany (Mathes and Schriefer, 1985). These ratios indicate that aboveground plant dark respiration can be as high as soil respiration.

In general, the calculated aboveground plant dark respiration followed a similar pattern in both 1987 and in 1988 (Fig. 7). The data from 1988 suggest that aboveground plant dark respiration was minor from October through April, but increased rapidly from the end of April until July and then decreased thereafter. This response is reasonably consistent with estimates of plant growth rate (Redmann, 1978a). A discrepancy between years occurred in June, when aboveground plant dark respiration was much higher in 1987 than in 1988. Precipitation was 415 mm from January through May of 1987 and only 172 mm during this same period in 1988, which could have led to early season plant biomass differences. It should be noted that the large respiration chambers used to determine whole-ecosystem respiration probably covered soil with a greater proportion of roots than small chambers, since root mass directly below crowns could be more substantial than between crowns. In the tallgrass prairie, however, distribution of grass clumps is much more uniform than in the shortgrass prairie, where organic matter enrichment of soil immediately under grass clumps can lead to greater potentially mineralizable C than between grass clumps (Burke et al., 1999).

From a tallgrass prairie in central Texas, soil respiration was predicted using soil temperature and soil water variables only, resulting in a coefficient of determination of 0.52 (Mielnick and Dugas, 2000). This regression equation without a plant growth effect in the model predicted soil respiration in our study with a coefficient of determination of only 0.33 (compared with 0.76 in our model that included a plant growth effect). To improve predictions of soil respiration using environmental variables, it appears necessary to include a plant growth effect,

which simulates changes in belowground C input. In our study, maximum plant growth effects on soil respiration were 77 and 92 mg CO_2-C m^{-2} h^{-1} in 1988 and 1987, respectively (Table 2; Fig. 5c,f). These values compare favorably to maximum plant growth effects on soil respiration in annually planted cropping systems in Texas (i.e., 70 to 150 mg CO_2-C m^{-2} h^{-1}; Franzluebbers et al., 1995).

The plant growth effect in our analyses is an empirical derivation that could be described more mechanistically with an actual estimate of plant growth rate. The daily rate of net photosynthesis or the rate of change in leaf area index would likely be reasonable descriptors of this effect.

SUMMARY AND CONCLUSIONS

Variation in both mean soil respiration and mean whole-ecosystem respiration at five locations in a tallgrass prairie in Kansas was positively related to soil organic C content ($r^2 = 0.71$). Variation in soil respiration and whole-ecosystem respiration among 79 nighttime sampling events during 2 yr was explained by temperature, WFPS, and a plant growth rate function ($r^2 = 0.76$ and 0.84, respectively). Combining analyses across 2 yr with differences in precipitation broadened the environmental conditions sampled and strengthened the deterministic relationship between environmental variables and respiration. Soil respiration and whole-ecosystem respiration increased significantly with increasing soil temperature only when WFPS was $\geq$0.4 m^3 m^{-3}. Conversely, only when soil temperature at 7 cm was $\geq$10°C, did soil respiration and whole-ecosystem respiration increase significantly with increasing WFPS. On the basis of temporal variograms, sampling events at ≈10-d intervals were optimum to minimize sampling cost and to maximize environmental changes that controlled soil and whole-ecosystem respiration. Future research on predicting soil respiration or whole-ecosystem respiration should mechanistically address the important role of plant growth on the supply of organic C substrates. We conclude that the contribution of soil respiration can be effectively separated from whole-ecosystem respiration in a tallgrass prairie through predictions with the regression equations developed and measurement of environmental (i.e., soil organic C, soil temperature, and WFPS) and physiological (i.e., plant growth rate) controls on soil C dynamics.

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Forest Floor Carbon and Nitrogen Losses Due to Prescription Fire

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ABSTRACT

Fire is the dominant factor affecting C and N losses from the semiarid forests of the eastern Sierra Nevada. As prescription fire becomes a best management practice, it is critical to develop an estimate of these fluxes. The objectives of this study were (i) to test and refine methods to estimate the volatilized C and N losses from the forest floor following fire, (ii) to investigate the interactions between O-horizon temperature and nutrient loss, and (iii) to assess measured N losses in the context of atmospheric N deposition, leaching, and N fixation. The quantities of C and N volatilized from the forest floor by prescription fire in the Sierra Nevada were measured using two different field-based methods: weight loss estimation and Ca/element ratio determination. Three sites were included in the study: Marlene, Sawtooth and Spooner. The weight method indicated C losses of 6.12, 7.39, and 17.8 Mg C ha^{-1} at the Sawtooth, Marlene, and Spooner sites, respectively. The ratio method indicated comparable C losses from the Sawtooth (6 Mg C ha^{-1}) site, but greater losses at Marlene (16 Mg C ha^{-1}) and Spooner (24 Mg C ha^{-1}) sites. The weight method indicated N losses of 56.2, 60.8, and 362 kg N ha^{-1}, at the Sawtooth, Marlene, and Spooner sites, respectively. The ratio method indicated comparable N losses of 59.9 kg N ha^{-1} at the Sawtooth site, but considerably greater losses at Marlene (243 kg N ha^{-1}), and Spooner (524 kg N ha^{-1}) sites. The Ca-element method was preferred because of minimal needs for preburn sampling. Regardless of method, the estimated losses were significant, particularly for N, compared with deposition and leaching rates. Volatilization will represent the major mechanism for N loss from forest ecosystems of this region subjected to prescribed fire.

Prior to settlement in the West, fire-recurrence intervals for Ponderosa pine (*Pinus ponderosa* Dougl. ex P. Lawson & Lawson) and Jeffery pine (*Pinus jeffreyii* Grev. and Balf.) sites varied from 2.5 to 15 yr and 14 to 18 yr, respectively (Dieterich, 1980). Postsettlement fire suppression began in the early 1900s. The buildup of fuel in understory and litter layers, and the subsequent devastating wildfires that have resulted have shown land managers the crucial role that periodic fire plays in an ecosystem. Increased stand density, low growth, increased susceptibility to disease, and species change can result from fire suppression (Kilgore, 1981). The accumulation of fuels has caused stagnation in nutrient cycling (Monleon and Cromack, 1996; Covington and Sackett, 1984) and an increase in fire potential. The need for forest management to create a defensible space at the urban–wildland interface has led to the adoption of prescribed fire.

Fires generate elevated O-horizon and soil temperatures, which can significantly disrupt ecosystem dynamics by altering nutrient budgets and cycling, as well as soil chemical and physical properties. The fluxes of nutrients (primarily C, N, S, and P) due to fire involve the oxidation of compounds to gaseous form, volatilization of organic matter, convection of ash particles, and water transport either by leaching or sediment transport (Binkley and Christensen, 1991).

Volatilized nutrient fluxes to the atmosphere have been estimated in several studies (Raison et al., 1985a; Feller, 1988; Jurgensen et al., 1981; Little and Ohmann, 1988; DeBell and Ralston, 1970). Losses are temperature dependent and a function of total material consumed. Globally, biomass burning may be a greater source of atmospheric CO_2 than all industrial outputs (Crutzen et al., 1979). Nitrogen is readily volatilized from foliage, even under low intensity burns (DeBell and Ralston, 1970; Knight, 1966). Sulfur loss from forest litter burned at 375 to 575°C was found to be from 24 to 79% of the total S in the remaining litter (Tiedemann, 1987). Temperatures in excess of 777°C are needed for complete volatilization of P (Raison et al., 1985a), and

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Abbreviations: NLTFPD, North Lake Tahoe Fire Protection District.